Aspects of the morphology and reproductive biology of the Australian Earless Dragon Lizard *Tympanocryptis tetraporophora*

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ABSTRACT

In the small Australian dragon (agamid) lizard *Tympanocryptis tetraporophora* mean snout-vent length (SVL) does not differ significantly between the sexes within the species as a whole. However, in a large sample from Sturt National Park, in northwestern New South Wales, males are larger than females both in snout-vent length and in mass. Large specimens are notably lacking from collections made during the coolest time of year.

The number of premaxillary teeth is not correlated with head size. However, the number of acrodont teeth on the maxilla and dentary increases with head size.

The modal number of presacral vertebrae is 23. There is no sexual dimorphism in either the number of postsacral vertebrae or the number of postsacral vertebrae with transverse processes. Hyperphalangy occurs in 3.2% of specimens. Gross variation in the sacral vertebrae occurs in 5.3% of specimens.

For allometric analysis, two samples were considered: specimens from Sturt National Park and all other specimens. Head length and hind limb length are each in negative allometry with snout-vent length in both samples. However, tail length is in isometry in both sexes in the Sturt sample but in positive allometry in males and negative allometry in females in the other specimens. Mass is in negative allometry with snout-vent length in males but in isometry in females in the Sturt sample. The residual variances around the regression are not significantly different between the sexes for head length, hind limb length and tail length in the Sturt sample, but the variances are significantly higher for females than for males for head length and hind limb length in the other specimens.

Ventral colours include both pale salmon and yellow hues. The salmon colour tends to diminish and the yellow colour to increase with increasing size. Females lack pale dorsal longitudinal stripes more often than males, perhaps because larger females lose the stripes whereas larger males do not. Only mature females ≥55 mm SVL are totally patternless, i.e., they lack both pale stripes and dark blotches.

Males and females become sexually mature at a SVL of approximately 42 mm and 46 mm, respectively. In the Sturt sample, testis size is much larger in spring that in autumn. In the species as a whole, reproduction occurs between early spring and mid-autumn. Females with yolking follicles or oviducal eggs range in size from 46.5 to 72.0 mm SVL with a mean of 58.0 mm. Clutch size ranges from 1 to 14 with a mean of 8.1. Clutch size is positively correlated with SVL.

Males are generally more common than females in collections, but the difference is statistically significant only among mature specimens. Comparisons are made with other Australian dragons.

Key words: Agamidae, Allometry, Australia, Reproduction, *Tympanocryptis*.

INTRODUCTION

The Earless Dragon *Tympanocryptis tetraporophora* (Fig. 1) is widely distributed over central and western New South Wales, northeastern South Australia and southcentral and southwestern Queensland (Fig. 2). The species' distribution outside this area (Cogger 1992) is uncertain, and hinges on the issue of the significance of a femoral pore (the primary diagnostic feature of the species) in a few specimens from the Northern Territory and northern Western Australia (Storr 1982). The species is relatively small in size, reaching a maximum snout-vent length of 72.5 mm. Although the species is primarily ground-dwelling, often seen sitting on the ground or on clods of earth along the side of the road, it can climb between one and two metres in low shrubs (P. Harlow and R. Sadlier, pers. comm.).

Recent survey work in Sturt National Park in the northwestern corner of New South Wales resulted in three valuable collections of *Tympanocryptis tetraporophora*: 10 specimens

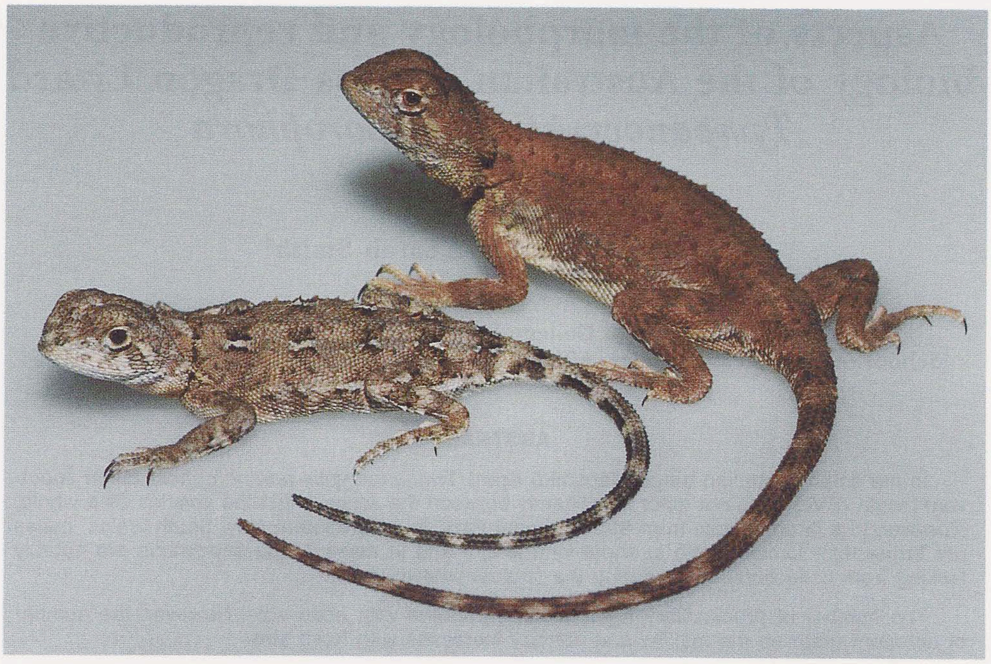

Fig. 1. Two specimens of *Tympanocryptis tetraporophora* (AM R 151669–151670) from Sturt National Park, New South Wales showing the two extremes of colour pattern. Both specimens are females.

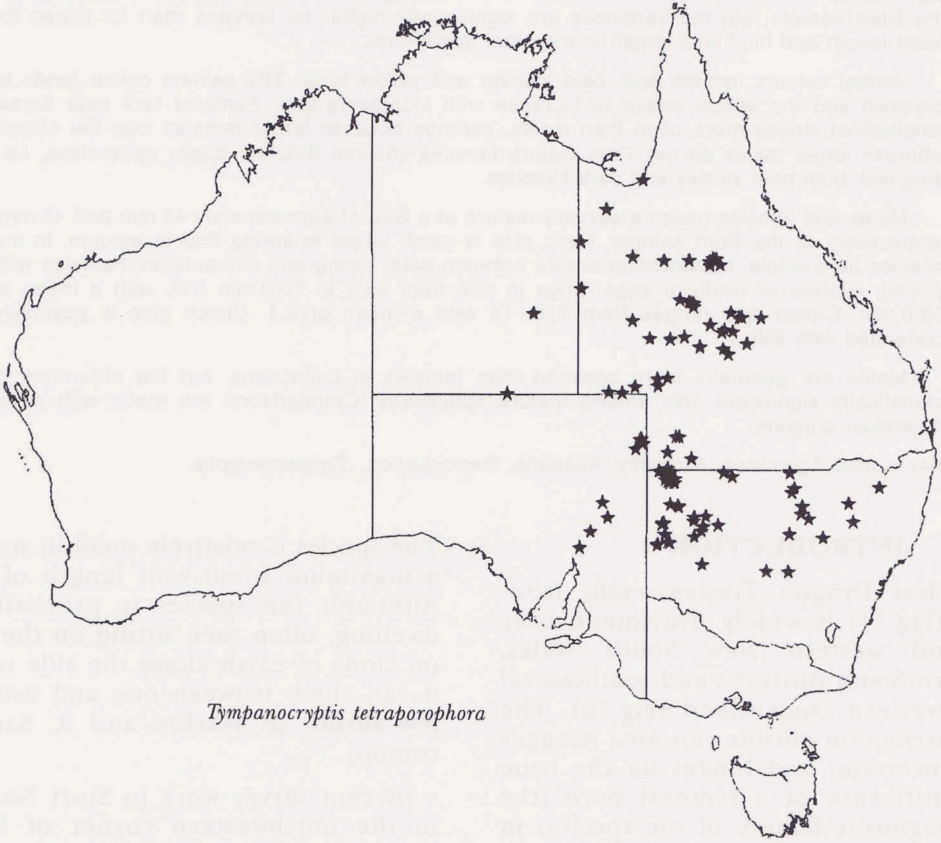

Fig. 2. The distribution of the *Tympanocryptis tetraporophora* specimens examined in this paper.

from early spring (25 September–3 October 1998; AM R 152872, 152885, 152936, 152948–152949, 1152953, 152962–152964, 152999); 25 specimens from mid-spring (27 October to 4 November 1997; AM R 151573, 151584–151585, 151604, 151606, 151621, 151669–151670, 151674, 151676, 151678–151680, 151700; AM field numbers 49500–49510), and 26 specimens from mid-autumn (9–12 April 1997; AM R 151127–151152). These specimens provided an opportunity to make detailed observations on ventral colour, the mass for freshly euthanased specimens, and the number of dentary teeth (the posterior of which are obscured by the maxilla in specimens preserved with the mouth closed). Data on these variables, especially mass, are rarely available for Australian dragons. Building on the opportunity provided by these three collections, all the specimens of *T. tetraporophora* in the Australian Museum (*n* = 249) and the Queensland Museum (*n* = 63) (Fig. 2) were examined for a variety of morphological variables. The results of this work are reported here.

MATERIALS AND METHODS

Colour notes were taken and mass (MA) determined to nearest 0.01 g on freshly euthanased animals. Specimens were fixed in 10% buffered formalin and stored in 70% ethanol. Most specimens were fixed with the mouth open to facilitate tooth counts, and fixed in a spread-eagle position to maximize information from radiographs

Snout-vent length (SVL), hind limb length (HLL), and tail length (TL) were measured to the nearest 0.5 mm by holding the preserved specimen against a steel rule. Head length (HDL), taken as the tip of the snout to the corner of the mouth, was measured to the nearest 0.1 mm with dial and digital callipers. The lack of a tympanum in this "earless" species precluded using this more traditional feature to define head length. Testis size, taken as the length of the left testis, was measured *in situ* under a dissecting microscope to the nearest 0.01 mm with digital callipers. Tails were assessed grossly under a dissecting microscope to assess whether they were intact or broken/regenerated. For the analysis of allometry measurements were transformed into base 10 logs.

The best method for investigating the allometric relationship between variables such as those in this study is reduced major axis regression (McArdle 1988). Unfortunately, the techniques for comparing regression lines is better understood for least squares regression (e.g., comparison of the elevations of slopes). Fortunately, however, as the correlation coefficient between any two variables rises, the regression lines of the two methods converge, and from a practical point of view they "virtually coincide" when $r > 0.90$ (McArdle 1988). The correlation coefficients for most of the variables analysed for allometry in this study are >0.90.

Maxillary and dentary teeth were counted on the left side only. Tooth sockets (pleurodont teeth) and worn tooth positions (acrodont) as well as actual teeth were counted.

The number of pre- and postsacral vertebrae, the number of postsacral vertebrae with transverse processes, and the number and symmetry of the sacral vertebrae were determined from radiographs.

Sex and state of maturity were determined by gross inspection of the gonads and associated efferent ducts, unless, in the case of males, the hemipenes were everted. Males were judged to be mature if they had relatively large testes and distinct tubules in the epididymes. Females were judged to be mature if they had yolking follicles or oviducal eggs and/or wide oviducts.

The allometry of mass on snout-vent length was only examined in the autumn (post-reproductive) Sturt sample in order to avoid possible seasonal effects.

All statistical analysis was carried out using Systat 6.0. The 0.05, 0.01, and 0.001 levels of statistical significance are indicated by the superscripts *, **, and ***, respectively. A lack of statistical significance in indicated by "ns".

The generic taxonomy follows Greer (1989b), but note that in that work, *Tympanocryptis tetraporophora* was mistakenly considered to be part of *T. lineata*.

RESULTS

Size

In the entire sample, snout-vent lengths range from 25.0 to 72.5 mm (*n* = 305). Males range from 27.5 to 72.5 mm (mean = 53.7, *n* = 157), and females range from 27.5 to 72.0 mm (mean = 50.1, *n* = 132). The sexes do not differ significantly in mean snout-vent length (Mann Whitney U = 11134^{ns}). Twenty-three specimens could not be sexed and/or measured accurately. The smallest specimens are from January and the largest from October–December. There are only a few specimens available from the period mid-May to mid-August, and all of those are relatively small (Fig. 3).

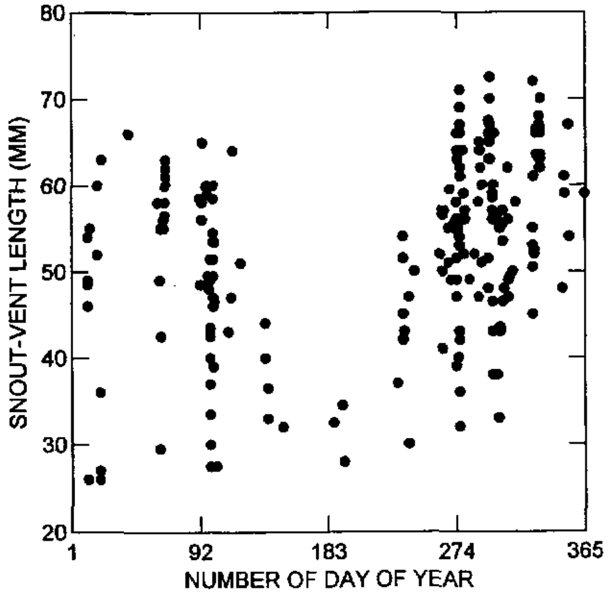

Fig. 3. The snout-vent length of *Tympanocryptis tetraporophora* in comparison to the number of the day of collection (1 January = 1 and 31 December = 365).

In the Sturt sample, snout-vent lengths range from 27.5 to 60.0 mm (n = 48). Males range from 30.0 to 60.0 mm (mean = 51.1, n = 37), and females range from 27.5 to 60.0 mm (mean = 44.0, n = 24). Males are significantly larger in mean snout-vent length than females (Mann Whitney U = 686***). Body mass ranges from 0.84 to 7.42 g (n = 48). Males range from 1.21 to 7.42 g (mean = 4.81, n = 32), and non-reproductive females range from 0.84 to 7.06 g (mean = 3.50, n = 13). Males are significantly heavier than non-reproductive females (Mann Whitney U = 333**).

Dentition

The premaxillary teeth are pleurodont and range in number from 2 to 4 (mode = 3, n = 58). The maxillary teeth include one (n = 5) or two (n = 95) anterior pleurodont teeth (the more posterior of which is usually longer) and 8 to 15 posterior acrodont teeth (n = 69). The dentary teeth include one (n = 2), two (n = 54, more posterior tooth usually longer), or three (n = 1, anterior and posterior teeth equal in size and middle tooth smaller) anterior pleurodont teeth and 9 to 16 posterior acrodont teeth (n = 53). The pleurodont teeth on the maxillary and dentary appear to be proportionately larger in males than in females (Greer, pers. obs).

There is no correlation between the number of premaxillary teeth and head length in either males (r = 0.10^{ns}, n = 40) or females (r = 0.09^{ns}, n = 26). However, there is a strong correlation between both the number of maxillary acrodont teeth and the number of dentary acrodont teeth, and head length. For the maxillary teeth, the correlation coefficients for males and females are, respectively: r = 0.84***, n = 37 and r = 0.89***, n = 26, and for the dentary teeth the correlation coefficients are, respectively: r = 0.87***, n = 28 and r = 0.88***, n = 19). The increase in the number of maxillary and dentary teeth with size is due to the addition of new teeth on the posterior (open) end of the tooth row on each bone (Greer, pers. obs).

Osteology

In the Sturt sample, the number of presacral vertebrae ranges from 22 to 24 (mean = 22.9, sd = 0.38, mode = 23, n = 60). The number of postsacral vertebrae ranges from 42 to 50 (mean = 45.7, sd = 1.73, n = 46). The number of postsacral vertebrae with transverse processes ranges from 27 to 45 (mean = 34.2, sd = 3.34, n = 56). There is no sexual dimorphism in either the number of postsacral vertebrae (t = 1.19^{ns}, df = 44) or the number of postsacral vertebrae with transverse processes (t = 1.77^{ns}, df = 54). There is no significant correlation between the number of postsacral vertebrae and the number of postsacral vertebrae with transverse processes in males (r = 0.05^{ns}, n = 25), but there is a strong correlation in females (r = 0.65**, n = 19).

In the Sturt sample, the phalangeal formula for the manus is 2.3.4.5.3 on both sides in 60 specimens and 2.3.4.6.3 on both sides in one (AM R 151136)(1.6%), i.e., an increase of one phalange in the fourth toe of the manus. The phalangeal formula for the pes is 2.3.4.5.3 on both sides in 60 specimens, and 2.3.4.5.3 on one side and 2.3.4.5.4 on the other in one specimen (AM R 151148)(1.6%), i.e., an increase (see below) of one phalange in the fifth toe of the pes on one side.

In the Sturt sample, the sacrum consists of two symmetric vertebrae in 58 specimens, but consists of one whole vertebra and two halves, one anteriorly and one posteriorly, in three specimens (AM R 151584, 151676, AM H 49508)(4.9%). In 19 additional specimens, the sacrum consists of two symmetric vertebrae, but in one (AM R 70091) it consists of just one vertebra (5.3%). Thus in the overall sample, 5% of the sacral vertebrae are "abnormal".

Allometry

Each case of allometry involving head length, hindlimb length and tail length on snout-vent length was examined in two samples: the smaller, regional sample from

Sturt National Park and the larger more widespread sample from the rest of the range, referred to here as the non-Sturt sample. This was to see if the smaller, regional sample, which is as close to a single interbreeding population as is available, could be taken as an indicator of the species as a whole. The allometry of mass on snout-vent length was examined in the autumn Sturt sample only. The results of the allometry analyses are presented in Table 1 and described briefly below.

For the relationship between log head length and log snout-vent length, the residual variance around the regression was not significantly different between the sexes in the Sturt sample, but it was significantly higher in females in the non-Sturt sample. This allowed further comparison of the regression lines between the sexes in the Sturt sample but precluded it in the non-Sturt sample. Comparison in the Sturt sample showed no significant difference between the sexes (Fig. 4) in either the slope or the intercepts of the regression lines; that is, the two lines were not significantly different and could be combined into one line representing both sexes. In both the Sturt and non-Sturt sample, the 95% confidence interval for the slope was less that the isometric value of 1.00 in all cases, indicating that head length is in negative allometry with snout-vent length; that is, head length becomes relatively smaller as snout-vent length increases.

For the relationship between log hind limb length and log snout-vent length, the residual variance around the regression was not significantly different between the sexes in the Sturt sample, but it was significantly higher in females in the non-Sturt sample. This allowed further comparison of the regression lines between the sexes in the Sturt sample but precluded it in the non-Sturt sample. Comparison in the Sturt sample showed no significant difference between the sexes (Fig. 5) in either the slope or the intercepts of the regression lines; that is, the two lines were not significantly different and could be combined into one line representing both sexes. In both the Sturt and non-Sturt sample, the 95% confidence interval for the slope was less that the isometric value of 1.00 in all cases, indicating that hind limb length is in negative allometry with snout-vent length; that is, hind limb length becomes relatively smaller as snout-vent length increases.

Table 1. Least square regression statistics for various allometric comparisons in the dragon lizard *Tympanocryptis tetraporophora*. The abbreviation "ci" is the 95% confidence interval for the slope of the regression. Regressions involving both sexes may include some unsexed specimens.

	Comparison of Regressions for Sexes (F values)						Regression Parameters				
	variances	df	slopes	df	intercepts	df	slope	ci	intercept	r^2	*n*
Log HDL on log SVL											
Sturt	1.79^{ns}	21,35	1.60^{ns}	56	21.66^{ns}	57	0.75	±0.05	–0.21	0.93^{***}	60
Non-Sturt	1.84^{*}	54,67	—	—	—	—	—	—	—	—	—
males	—	—	—	—	—	—	0.77	±0.04	-0.23	0.96^{***}	69
females	—	—	—	—	—	—	0.62	±0.06	0.003	0.88^{***}	56
all specimens	—	—	—	—	—	—	0.73	±0.03	–0.17	0.93^{***}	134
Log HLL on log SVL											
Sturt	1.27^{ns}	22,35	1.54^{ns}	57	1.91^{ns}	58	0.85	±0.07	0.10	0.92^{***}	61
Non-Sturt	1.59^{*}	72,84	—	—	—	—	—	—	—	—	—
males	—	—	—	—	—	—	0.84	±0.05	0.11	0.92^{***}	86
females	—	—	—	—	—	—	0.79	±0.07	0.16	0.88^{***}	74
all specimens	—	—	—	—	—	—	0.87	±0.04	0.05	0.90^{***}	173
Log TL on log SVL											
Sturt	1.14^{ns}	22,34	3.85^{ns}	56	9.98^{**}	57	—	—	—	—	—
males	—	—	—	—	—	—	1.14	±0.14	–0.05	0.90^{***}	34
females	—	—	—	—	—	—	0.95	±0.14	0.25	0.90^{***}	22
Non-Sturt	1.46^{ns}	92,109	36.98^{***}	201	—	—	—	—	—	—	—
males	—	—	—	—	—	—	1.17	±0.06	-0.08	0.93^{***}	111
females	—	—	—	—	—	—	0.87	±0.08	0.37	0.84^{***}	94
Log MA on log SVL											
Sturt	1.16^{ns}	6,13	5.83^{*}	19	—	—	—	—	—	—	—
males	—	—	—	—	—	—	2.65	±0.26	–3.84	0.97^{***}	15
females	—	—	—	—	—	—	3.08	±0.33	–4.51	0.99^{***}	8

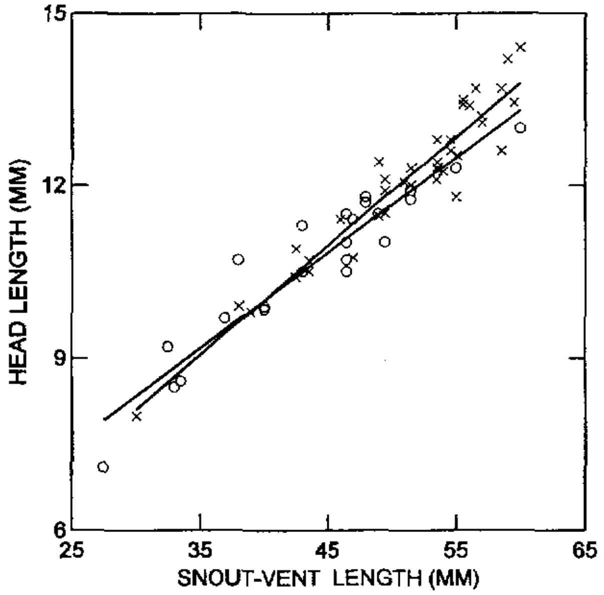

Fig. 4. Plot of the regression of head length on snout-vent length for the sexes in the Sturt sample of *Tympanocryptis tetraporophora*. Data not transformed. Symbols: males — x; females — o.

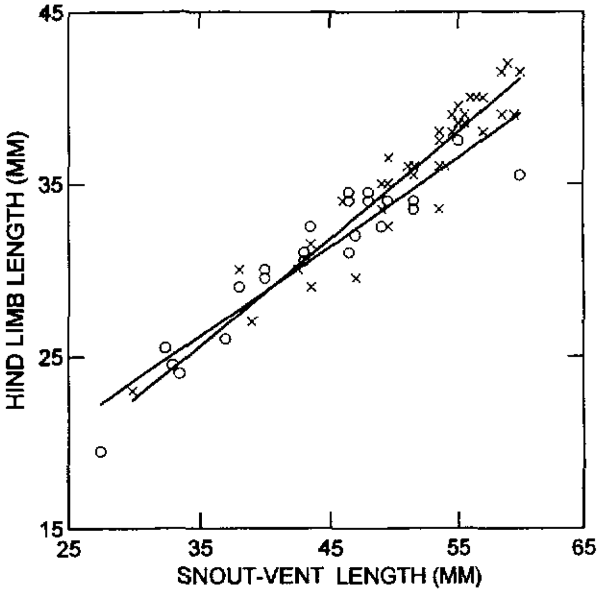

Fig. 5. Plot of the regression of hind limb length on snout-vent length for the sexes in the Sturt sample of *Tympanocryptis tetraporophora*. Data not transformed. Symbols: males — x; females — o.

For the relationship between log tail length and log snout-vent length, the residual variance around the regression was not significantly different between the sexes in either the Sturt sample or the non-Sturt sample. This allowed further comparison of the regression lines between the sexes in both samples. In the Sturt sample, the slopes of the regression were not significantly different between the sexes, but females had a significantly higher intercept. In the non-Sturt sample, the slope was significantly higher in males than in females. However, it may be prudent to reserve judgement on the results in both samples. In the Sturt sample, the actual value for the slope is higher in males than in females (as it is in the non-Sturt sample)(Fig. 6) and the significance level for the difference between the slopes is very low, P = 0.054. And in the non-Sturt sample, the difference between the sexes in the residual variances of the regressions is just significant (P = 0.05+). In the Sturt sample, the 95% confidence interval of the slope includes the isometric value of 1.00 in both males and females, although just so for males, and in the non-Sturt sample, the confidence interval falls above the isometric value in males but below in females. These results suggest that in the Sturt sample, tail length is in isometry with snout-vent length in both sexes, although just so in males, and that in the non-Sturt sample, tail length is in positive allometry in males and in negative allometry in females. In other words in the Sturt sample, both sexes maintain relative tail length with increasing snout-vent length, but in the non-Sturt sample, males have relatively longer tails and females relative shorter tails with increasing snout-vent length.

In the autumn Sturt sample, the residual variance of the regression of log mass on log snout-vent length was not significantly different between the sexes, making a comparison of the regression lines appropriate. This comparison showed that females have a significantly higher slope than males (Fig. 7). The 95% confidence intervals for the slopes of the regression for males and for females fall below and above, respectively, the isometric value of 3.00, suggesting that mass is in negative allometry with snout-vent length in males but in isometry in females. In other words, the males become relatively lighter in mass with increasing snout-vent length but females maintain their relative mass.

Colour

Judging from specimens from Sturt, pale salmon and yellow colour hues occur on the throat and ventral body (generally anteriorly) in most specimens. The two colours can occur separately or together. When the two colours occur together they may combine to give a orange hue or they may remain separate in which case the salmon colour tends to occur peripherally and the yellow centrally. The colours occur in specimens collected both in spring and autumn. The only specimens that did not show any ventral colour whatsoever were the smallest specimen (SVL = 27.5), an autumn juvenile, and one of the largest

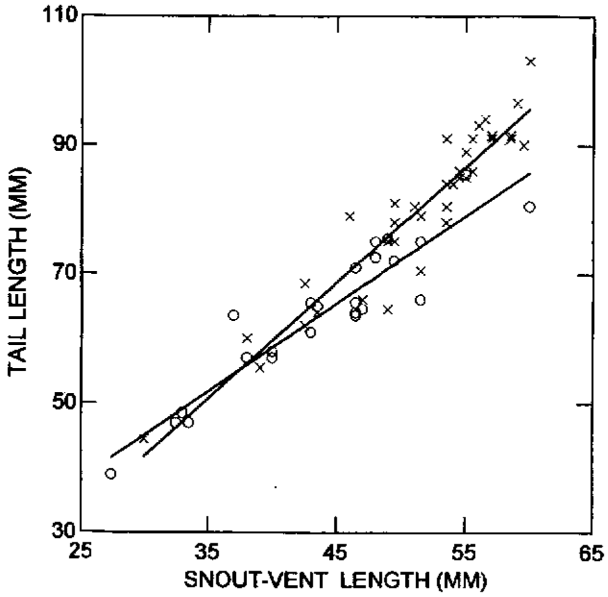

Fig. 6. Plot of the regression of tail length on snout-vent length for the sexes in the Sturt sample of *Tympanocryptis tetraporophora*. Data not transformed. Symbols: males — x; females — o.

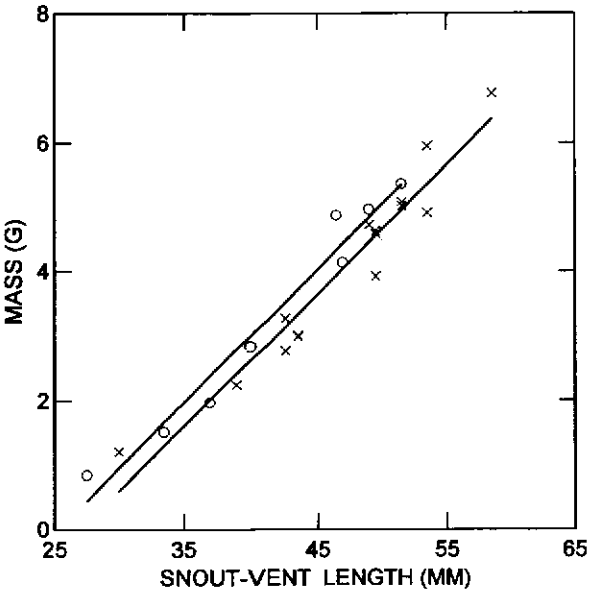

Fig. 7. Plot of the regression of mass on snout-vent length for the sexes in the autumn (post-reproductive) Sturt sample of *Tympanocryptis tetraporophora*. Data not transformed. Symbols: males — x; females — o.

(SVL = 59.5 mm), a spring male with large turgid testes. All specimens ≥30.0 SVL except the spring male just mentioned had some throat colour, but several specimens of both sexes between 37 and 59.5 mm SVL lacked ventral body colour.

Arranging these two colours in the sequence with size that was indicated on general inspection of the specimens: colourless → salmon → mixed → yellow, there was no correlation between throat colour and snout-vent length in males inclusive of the large colourless male mentioned above ($r^s = 0.24^{ns}$, $n = 31$) but there was a significant correlation exclusive of this male ($r^s = 0.38^*$, $n = 30$); there was also a very strong correlation in females ($r^s = 0.78^{***}$, $n = 18$). In terms of chest colour arranged similarly, there was no correlation with snout-vent length in all males ($r^s = -0.03^{ns}$, $n = 31$), all males exclusive of the one mentioned above ($r^s = 0.07^{ns}$, $n = 31$), and all females ($r^s = 0.36^{ns}$, $n = 18$). All these correlations still pertain when the analysis is carried out by season, that is spring and autumn, with the exception that both spring and autumn males each show no significant correlation between throat colour and size. These ventral colours are transient in 70% alcohol and disappear totally within 11 months (perhaps much sooner).

Casual inspection of any large series of the species indicates that whereas most specimens have pale longitudinal mid-dorsal and lateral dorsal stripes, some specimens do not (Fig. 1; Greer 1989b; fig. 16, as *Tympanocryptis lineata*). These latter specimens often even lack the dark blotches on the dorsum and therefore appear to be almost uniform in colour, that is, patternless. The stripeless pattern is significantly more common in females (39 of 79) than in males (10 of 102)($X^2 = 35.29^{***}$). Furthermore, the striped pattern appears to be constant with age in males, but tends to be absent in larger females. For example, there is no significance size difference between striped and stripeless specimens in males ($t = 0.67^{ns}$, df = 100), but stripeless specimens are larger than striped specimens in females ($t = 3.12^{**}$, df = 76). Furthermore, all completely patternless (no stripes or dark blotches) specimens ($n = 12$) are females ≥55 mm SVL.

The colour of the mouth and tongue in the species is pink.

Reproduction

The smallest male judged to be mature had a SVL of 37 mm, which seems very small. Otherwise, all males ≥42 mm SVL were mature with one possible exception. This specimen, from the far northern locality of Kuranda, had a SVL of 47 mm and appeared to be either just coming into maturity or mature but quiescent. A snout-vent length of 42 mm is taken here as the size of maturity for males. In the Sturt sample, the only sample representing large spring and autumn series, testis size was much larger in spring (25 September–4 November) than in autumn (9–12 April)(Fig. 8).

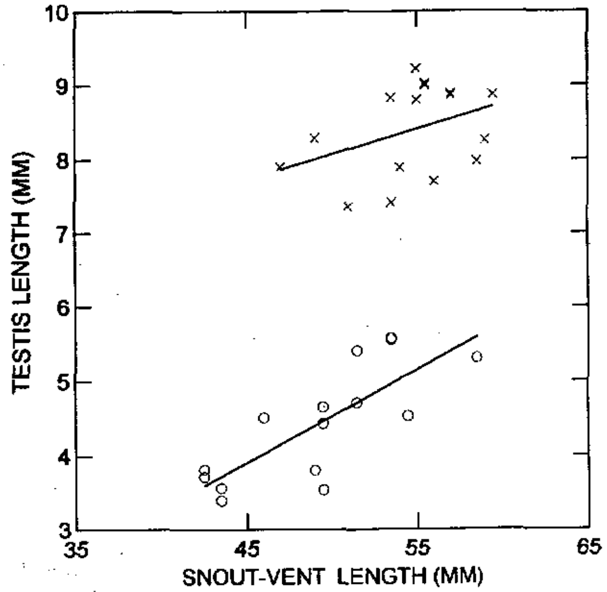

Fig. 8. Plot of testis length and snout-vent length in spring (x) and autumn (o) male *Tympanocryptis tetraporophora* from Sturt National Park.

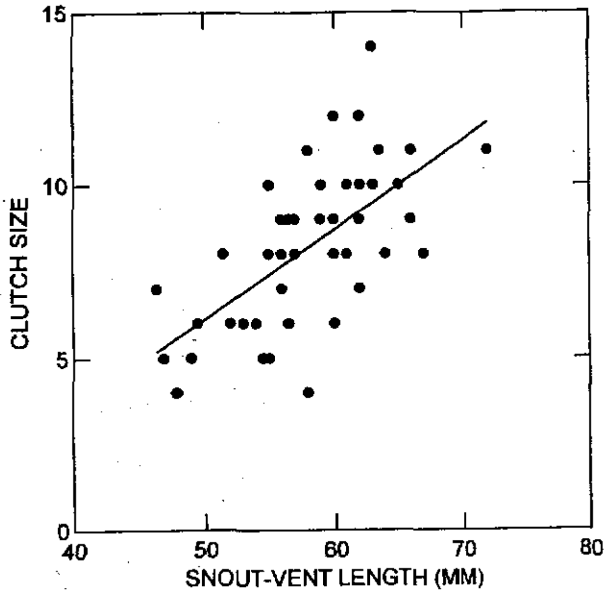

Fig. 9. Plot of the relationship between clutch size and female size in *Tympanocryptis tetraporophora.*

Females containing yolking ovarian follicles were collected between 21 September and 7 April (n = 13). These include two autumn dates, 3 March (QM 47769) and 7 April (QM J 47676), both from central and northern Queensland: Brendallan Station near Aramac (22°57'S) and 67 km S of Burketown (18°38'S), respectively. Females carrying shelled oviducal eggs were collected between 3 October and 24 April (n = 23). These include two mid-autumn dates, 3 April (QM 47830–47831) and 24 April (QM J 47792), both from central and northern Queensland: 10 km E of Longreach (23°27'S) "Tirranna Roadhouse via Burketown" (precise locality not found), respectively.

Females with either yolking ovarian follicles or oviducal eggs range in snout-vent length from 46.5 to 72.0 mm (mean = 58.0, sd = 5.31, n = 61). A snout-vent length of 46.5 mm is taken here as the size of maturity for females. Clutch size based on both yolking follicles and oviducal eggs ranges from 1 to 14 (mean = 8.1, sd = 2.41, n = 50), or 4 to 14 (mean = 8.2, sd = 2.20, n = 49) if the single specimen with a clutch size of one is considered aberrant. The snout-vent lengths for females with countable clutches (above) range from 46.5 to 72.0 mm (mean = 58.3, sd = 5.40, n = 50). There is a significant correlation between female snout-vent length and clutch size ($r = 0.63^{***}$, n = 48). The regression equation for the relationship is clutch size = -5.40 + 0.23 female snout-vent length ($r^2 = 0.27^{***}$, n = 50) including the female with a clutch size of one (SVL = 63 mm), and clutch size = - 6.85 + 0.26 female snout-vent length ($r^2 = 0.40^{***}$, n = 49, Fig. 9) excluding this female. The oviducal eggs appear to fill the entire body cavity and give the impression of being very tightly "packed".

Sex ratio

Males are more numerous than females both in the entire sample (157 vs 133) and in the Sturt sample (37 vs 24), but in neither case is the difference significant ($X^2 = 1.98^{ns}$ and 2.77^{ns}, respectively). However, in the entire sample, specimens as large or larger than the size at which females become mature, 46.5 mm SVL, males are significantly more numerous than females (129 vs 95; $X^2 = 4.09^{*}$), but in specimens smaller than this, males are less numerous than females (32 vs 37) but not significantly so ($X^2 = 0.36^{ns}$)

DISCUSSION

Size

The discrepancy between the lack of sexual dimorphism in size in the whole sample of *Tympanocryptis tetraporophora* and the marked sexual dimorphism (males larger) in the Sturt sample may be due to sampling bias or to geographic variation. Unfortunately no other large samples are available for comparison. However, from a practical point of view, this result shows that species-wide and population samples can differ, and hence one may not reflect the other.

Assuming the population sample is the more biologically relevant form of the variable, the strong sexual size dimorphism in the Sturt sample (males larger) can be compared to the data available for other small dragons. For example, in a population of *Ctenophorus femoralis* (*n* = 31), males were significantly larger than females in mean snout-vent length (Greer 1989a). However, in a central New South Wales population of the closely related *C. fordi*, "females tend to be somewhat larger than males" (Cogger 1974). Furthermore, in a population of *Rankinia adelaidensis* near Perth, females were significantly larger than males in mean snout-vent length (Bamford 1992).

With regard to sexual size dimorphism in other species-wide samples (no sexual size dimorphism in *Tympanocryptis tetraporphora*), data for three other small species of dragons suggest that there is no significant sexual size dimorphism in two species of *Diporiphora* but that females are significantly larger than males in *Rankinia diemensis* (Greer, pers. obs. on museum specimens). In *Diporiphora australis* from eastern Australia males range in SVL from 26 to 77 mm with a mean of 51.5 mm (*n* = 208) and females range from 30.5 to 74 mm with a mean of 50.9 mm (*n* = 149) (Mann Whitney U = 16287^{ns}). In *D. magna* from northern Australia, males range in SVL from 26 to 90 mm with a mean of 59.3 mm (*n* = 105) and females range from 32.5 to 77.5 mm with a mean of 55.6 mm (*n* = 63) (Mann Whitney U = 3841^{ns}). However, in *Rankinia diemensis* from southeastern Australia, females are significantly larger than males: males range in SVL from 26 to 67 mm with a mean of 49.3 mm (*n* = 47) and females range from 27 to 82 mm with a mean of 58.3 mm (*n* = 79)(Mann Whitney U = 1010^{***}).

In general, these results suggest that in relatively small dragons all three conditions of sexual size dimorphism exist (males larger than females, females larger than males, and no significant difference in size between the sexes). These results indicate a potentially diverse variety of influences on size in the sexes in small dragons.

The dearth of large specimens of *Tympanocryptis tetraporphora* between mid-May and mid-August (Fig. 3) can be interpreted in two ways. First, most if not all of the adults may die before winter. This is plausible because other species of dragons experience extremely high levels of adult mortality at the end of the activity season, including some species that are larger in size than *Tympanocryptis tetraporophora*, e.g., *Ctenophorus caudicinctus* (Bradshaw *et al.* 1991), and *C. nuchalis* (Bradshaw 1986). Second, only small individuals may be active during winter. In order to distinguish between these two alternatives, more detailed monitoring of a single population is needed.

Dentition

The dentition of *Tympanocryptis tetraporophora* is broadly similar to other agamids in the distribution of pleurodont and acrodont teeth on the jaw bones, the relatively little variation in the number of premaxillary teeth, and the increasing number of acrodont teeth on the maxilla and dentary with growth (Cooper *et al.* 1970).

As in *Tympanocryptis tetraporophora*, the larger species of *Tympanocryptis* appear to have two as the modal number of pleurodont teeth on the maxilla, i.e., *T. cephala* (two teeth in 12 specimens and one tooth in one specimen), *T. intima* (2 in 7 and 1 in 2), *T. lineata centralis* (2 in 16), and *T. lineata houstoni* (2 in 14 and 0 in 1). In contrast, the smaller species generally have only one pleurodont tooth on the maxilla, i.e., *T. butleri* (1 in 6 and 2 in 1) and *T. parviceps* (1 in 11).

Other small dragons also seem to usually have only one pleurodont tooth on the maxilla. For example, this is the condition in *Ctenophorus femoralis* (one tooth in 25 specimens and two teeth in two specimens), *C. fordi* (0 in 1, 1 in 17, 2 in 1), *Rankinia adelaidensis* (1 in 4), and *R. chapmani* (1 in 1).

Osteology

In general, there are two different modal values for the number of presacral vertebrae in *Tympanocryptis* (Table 2). The group consisting of *T. cephala*, *T. lineata*, and *T. tetraporophora* has a modal number of 23 whereas the group consisting of *T. butleri* and *T. parviceps* has a modal number of 22. The modal number may be related to size, as the first group with one more presacral vertebra modally consists of large species whereas the second group consists of small species. In other words, a contributing factor to a difference in size in *Tympanocryptis* may be the number of presacral vertebrae.

The range and mean number of postsacral vertebrae found here for *Tympanocryptis tetraporophora* (42–50, 45.9) corroborates the results of an earlier study of this species (41–50, 46; Mitchell 1948).

The six phalanges present bilaterally in the fourth toe of the manus of one specimen of *Tympanocryptis tetraporophora* is an obvious increase in the number of phalanges from what is the common, and almost certainly primitive condition both for squamates in general and agamids in particular, of five

Table 2. Number of pre- and post-sacral vertebrae in six species (one with three subspecies) of *Tympanocryptis*.

	Pre-sacral				Post-sacral		
Species	Range	Mean	Mode	*n*	Range	Mean	*n*
Tympanocryptis							
butleri	21.5–22.5	22.0	22	7	38–41	39.4	6
cephala	22–24	22.8	23	22	37–43	40.6	6
intima	22–23	22.8	23	8	39–46	42.3	2
lineata							
centralis	23–24	23.0	23	11	43–47	44.6	5
houstoni	22–24	22.8	23	15	45–50	47.5	8
pinguicolla	22.5–24	23.3	23/24	5	48	48.0	2
parviceps	21–23	22.2	22	13	38–42	39.7	11
tetraporophora	22–24	22.9	23	60	42–50	45.7	46

phalanges. This is the first record of hyperphalangy in the manus of any agamid (Greer 1992). The only other known case of hyperphalangy in agamids is as an occasional extra phalange in the fourth digit of the pes in the Australian *Ctenophorus femoralis* (Greer 1989a).

The four phalanges in one pes of one specimen of *Tympanocryptis tetraporophora* represents a very probable "reversal" to the primitive agamid condition, in that the primitive condition for *Tympanocryptis* is likely to have been three phalanges (Greer 1989b). A similar possible "reversal" has been observed bilaterally in a specimen of *T. butleri* (Greer 1987b), and in a specimen of *Ctenophorus clayi* (Greer 1987a). Perhaps the primary significance of these individual increases in the number of phalanges is that they provide further examples (Greer 1992) of the kind of variation that could lead to an increase in the number of phalanges in evolution, and perhaps even to the occasional reversal of limb reduction.

Of the two unusual variations in the sacral vertebrae seen in *Tympanocryptis tetraporophora*, a single sacral vertebra (1.3%) and one whole sacral vertebra with a half vertebra both anteriorly and posteriorly (3.7%), only the latter has been seen in other species of the genus. Variations in the sacral complex found in other species of *Tympanocryptis* were as follows (all Australian Museum specimens): among seven *T. butleri* examined, two specimens had an asymmetrical sacral complex consisting of one whole vertebrae and two halves, one anteriorly and one posteriorly (29%); among 27 *T. cephala*, one specimen also had a similarly asymmetrical sacral complex consisting of one whole vertebrae and two halves, one anteriorly and one posteriorly, and another specimen had three symmetrical sacral vertebrae (7%), and among 16 *T. lineata centralis*, one specimen had an asymmetrical sacral complex consisting of two sacral vertebrae and one half of the first postsacral (6%). All other *Tympanocryptis* examined had two symmetrical sacral vertebrae: *T. intima* ($n = 11$), *T. l. housteni* ($n = 16$), *T. l. pinguicolla* ($n = 5$), and *T. parviceps* ($n = 9$). Whether these variations in the sacral complex impair function, especially locomotion, is unknown. However, to judge from their seemingly high frequency in some of the species, they are unlikely to be too debilitating.

Allometry

Most earlier studies of allometry in Australian dragons either did not examine the possibility that the sexes differ in their allometric parameters (Witten 1982, 1985; Witten and Coventry 1984, 1990; Johnston 1992; Peterson *et al.* 1994), or did not test the statistical significance of the purported differences (Storr 1966; Houston 1974; Witten 1994). Only three studies have adequately addressed these issues in dragon lizards. In *Ctenophorus nuchalis* no differences were found between the sexes in snout-vent length, tail length, front limb span, hind limb span, or thigh mass compared to total mass (Garland 1985). In *Ctenophorus nuchalis* males increased in weight more rapidly than females (Bradshaw and De'ath 1991). In *Chlamydosaurus kingii* males had relatively longer head lengths, head widths and frill lengths than females (Christian *et al.* 1995). These latter two studies plus the finding here that the sexes of *Tympanocryptis tetraporophora* can differ significantly in some statistical parameters, such as the residual variance of the regression of both head length and hind limb length on snout-vent length, and in certain aspects of their allometry, such as tail length and mass on snout-vent length, suggests that it may be useful to compare the sexes as a first step in future allometric work.

The negative allometry of head length with snout-vent length found in both sexes in both samples of *Tympanocryptis* *tetraporophora* also occurs in most other Australian dragon species in which the relationship has been examined (Witten 1982, 1985; Witten and Coventry 1984, 1990; Johnston 1992; Peterson *et al.* 1994). However, head length is in isometry with snout-vent length in *C. vadnappa* (Johnston 1992), and perhaps also in *Diporiphora bennettii* and *Lophognathus longirostris* (Witten 1982). The negative allometry of head length on snout-vent length is a general feature of amniotes (Rensch 1959). This makes the dragon species that seem to be exceptions to this trend worthy of further examination.

The negative allometry of hind limb length with snout-vent length found here for both sexes in both samples of *Tympanocryptis tetraporophora* is in contrast to an earlier finding of isometry for the species (Witten 1982). The discrepancy between this study and Witten's may be related to sample size: 61 and 173 in the Sturt and the non-Sturt samples, respectively, in this study vs 17 in Witten's study. In all other species of *Tympanocryptis* examined to date, the hind limb is in isometry with snout-vent length, i.e., *T. cephala* and *T. intima* (Witten 1982). Both negative allometry and isometry of hind limb length with snout-vent length are widespread among Australian dragons, but with no clear ecological trends (Witten 1982, 1985; Witten and Coventry 1984, 1990; Johnston 1992; Peterson *et al.* 1994). Positive allometry is known only in *Amphibolurus nobbi* and *Diporiphora bennettii* (Witten 1982, 1985).

The isometry of tail length with snout-vent length found here for the Sturt sample of *Tympanocryptis tetraporophora* confirms an earlier indication of isometry for the species (Witten 1982). The result of positive allometry in males in the non-Sturt sample is similar to other species of *Tympanocryptis* which show positive allometry, i.e., *T. cephala* and *T. intima* (Witten 1982, 1985). The finding of negative allometry in females in the non-Sturt sample has not been observed in any other species of *Tympanocryptis*. Both isometry and positive allometry of tail length with snout-vent length are widespread among other Australian dragons, but with no clear ecological trends (Witten 1982, 1985; Witten and Coventry 1990; Johnston 1992; Peterson *et al.* 1994). The only dragons reported to have negative tail allometry are *Lophognathus longirostris* (Witten 1982, 1985) and some populations of *Pogona vitticeps* (Witten and Coventry 1990). However, recent work with a larger sample size has shown that *Lophognathus longirostris* has positive tail allometry in males and isometry in females (A. Tulloch, pers. comm.). This leaves only female *Tympanocryptis tetraporophora* and *Pogona vitticeps* with negative tail allometry. The common, but not exclusive feature of these two forms, is relatively sedentary habits. This suggests that a tail which becomes relatively shorter with increasing body length may be advantageous in forms in which infrequent, short dashes are the maximum locomotor activity.

The negative allometry in males and the isometry in females for the relationship between mass and snout-vent length in *Tympanocryptis tetraporophora* differs from the results of the two other comparable analyses of the relationship between these two variables in Australian dragons. In *Ctenophorus nuchalis*, the sexes did not differ in their allometry of snout-vent on mass, and the sexes combined showed a very slight positive allometry, the 95% confidence interval of the slope of 0.346, ± 0.010, just failing to include the isometric value of 0.333 (Garland 1985). In *Ctenophorus nuchalis*, males had a significantly higher slope than females for mass on snout-vent length, but not enough detail was given to establish the nature of the allometric relationship in either sex (Bradshaw and De'ath 1991).

The significantly higher residual variance around the regression of head length and hindlimb length on snout-vent length in females compared to males in the non-Sturt sample is intriguing but difficult to explain. One possibility is that females are subject to more geographical selection (variation) than are males. This could be tested by more detailed comparisons between the sexes in more geographical widespread populations.

In general, the results of the allometric analyses were not strikingly different between the Sturt and non-Sturt samples. The allometries for head length and hind limb length on snout-vent length were negative in all cases in both samples. The analyses for the allometry for tail length on snout-vent length had border-line significant values that make the interpretation slightly equivocal in both samples (difference between slopes in the Sturt sample and the residual variances in the non-Sturt sample), but one similarity was the absolutely higher value of the slopes for males compared to females in both samples.

Colour

Previously there was no published information on ventral colour in this species. However, the Sturt sample, representing both spring and autumn specimens, indicates that ventral colour hues consisting of pale salmon and/or yellow are conspicuous on the throat and chest in most specimens. These ventral colours rival in intensity those of any other species of Australian dragons. The tendency on the throat for the amount of salmon colour to decrease and the amount of yellow colour to increase with size in both sexes (spring and autumn combined) is difficult to explain. Also, why the relationship should be stronger in females than in males is unclear (for the combined spring and summer sample the r_s value is much higher in females than in males and the correlation breaks down in spring and autumn males analysed separately, $n = 17$ and 14, respectively, in contrast to spring and autumn females, $n = 10$ and 8, respectively).

The occurrence of ventral colour hues in specimens from autumn, that is, late in the activity season, is especially intriguing. If the colours are related to breeding, are they residual from the past breeding season, or are they in anticipation of the next season which would appear to start no earlier than September judging from females with the earliest yolking and oviducal eggs (3 October in both cases)? Or is it possible that colours have a non-reproductive function at the close of the activity season?

The few notes available on ventral colour in other species of *Tympanocryptis* indicate that at least some may have some ventral colour. In *T. butleri* the chin and lips are described as "yellow" (Storr *et al.* 1983) and the tip of the chin as "bright yellow" in some specimens (Greer 1987b). A specimen of *T. l. lineata* from western Eyre Peninsula had a "bright yellow chin and lower lips" (Houston 1978), and breeding colours in male *T. l. pinguicolla* consist of bright yellow in the gular region and distinct pink in the pelvic region (Jenkins and Bartell 1980; see also their figure on page 97) and "bright yellow markings in the gular region and a pink suffusion on the sides of the body" (Osborne *et al.* 1993). *T. parviceps* females had the underside of the tail "pale yellow" but males lacked this colour (Greer 1987b).

These observations suggest that distinct yellow colour is a feature of at least some species of *Tympanocryptis*, although it may occur on different parts of the body. The species most similar in colour pattern to *T. tetraporophora* is *T. lineata pinguicolla*. Both species share yellow on the throat and a pinkish hue on the venter of the body. However, in *T. tetraporophora* the yellow appears to be more extensive (occurring on the chest in some specimens), and the pink (salmon) appears to occur more anteriorly (on the chest) instead of more posteriorly.

The apparent loss of the striped pattern in larger females may be related to reproduction. On gross inspection, females are extremely "full" of eggs, and it may be that this "burden" causes a change in either their behaviour or their choice of microhabitat which in turn makes a change of pattern advantageous.

Reproduction

In the Sturt sample, the much larger testis size in spring compared to autumn (Fig. 8) suggests that mating occurs in spring but not in autumn. Spring to early summer mating is also the norm for other dragons in temperate Australia, e.g., *Ctenophorus fordi* (Cogger 1978), *C. isolepis* (Pianka 1971), *C. maculosus* (Mitchell 1973), and *C. ornatus* (Bradshaw 1971).

The earliest date for a female *Tympanocryptis tetraporophora* with yolking ovarian eggs is 21 September and the latest date is 7 April. The earliest date for a female with oviducal eggs is 3 October and the latest date is 24 April. Nothing is known about the incubation period in *Tympanocryptis*, but assuming, conservatively, a fairly short incubation period of 30 days, it is unlikely that the hatchlings of this late April female would have emerged from their nest before late May. At the probable locality of this specimen (near Burketown, Queensland), the projected hatching date for the eggs would have been in the transition period from the wet season to the dry season.

There is some indication that the breeding season may extend later into the year in the north than the south. For example, dividing the species' range into about equal sized southern and northern parts at 26°S latitude (the latitude of the northern border of South Australia), the latest date for ovarian eggs in the south is 19 January but two dates exceed this in the north: 3 March (QM J 46679) and 7 April (QM J 47676). Similarly, the latest dates for oviducal eggs in the south is 8 March but two dates exceed this in the north: 3 April (QM J 47830–31) and 24 April (QM J 47792). There is insufficient material from the northern part of the range to assess the beginning of the reproductive season in this area. However, a female collected from 35 km north-west of Winton (at approximately 22°08'S) on 10 October that was "heavily gravid" (Valentic and Turner 1998) suggests reproduction is underway by at least mid-spring.

The only other observation of the seasonality of reproduction in this species is that eggs are laid in February and March (presumably based on specimens from

Table 3. Female size and clutch size in six species (one with two subspecies) of *Tympanocryptis*. The values in bold were used in the analysis of the relationship between mean female size and mean clutch size described in the text and shown in Figure 10. All data are based on personal observation.

	Snout-vent length (mm)			Clutch size		
Species	Range	Mean	*n*	Range	Mean	*n*
Tympanocryptis						
butleri	42–45	**43.5**	2	2	**2.0**	2
cephala	50–56	**53.6**	7	4–12	**7.8**	7
intima	55–59	**57.0**	3	8–10	**8.7**	3
lineata						
centralis	52–61	**55.5**	9	5–8	**7.3**	9
houstoni	41–59	**53.2**	7	2–8	**5.7**	7
parviceps	42–52	**45.6**	5	2–3	**2.2**	5
tetraporophora	47–72	**58.3**	50	1–14	**8.1**	50

northcentral South Australia; Lucas and Frost 1896), dates that accord well with the results obtained in this study for the southern part of the range (as defined above). The clutch size reported here for the species, 1 to 14 or 4 to 14 if the only specimen with less than four eggs is excluded, is also inclusive of the only other reported clutch size of 9 to 12 (Lucas and Frost 1896).

The strong correlation between female size and clutch size found for *Tympanocryptis tetraporophora* is typical of many, but not all, Australian dragons (Greer 1989b).

Data on gravid female size and clutch size in *Tympanocryptis* were omitted in a recent review of Australian dragon biology (Greer 1989b) and are presented here (Table 3). Least squares regression analysis of mean clutch size on mean female size for species and subspecies of *Tympanocryptis* shows that there is a very strong relationship between the two variables ($r^2 = 0.93^{***}$, $n = 7$, Fig. 10), and that the slope is very steep (0.48). This slope suggests that, in speciation, a change in the mean adult female size of just over 2 mm can lead to a change in the mean clutch size of one. In other words, mean clutch size can change markedly up or down with relatively little change in mean body size.

Sex ratio

The tendency in *Tympanocryptis tetraporophora* for males to be more numerous than females in samples containing largely mature specimens is in the same direction as all but one of the significantly different cases indicated by data in the literature for Australian dragons (Table 4). The only exception, aside from two of several monthly samples in a two year study of *Ctenophorus fordi*, appears to be *Rankinia diemensis* in which females are more numerous than males.

There are two non-mutually exclusive explanations for the general preponderance of males over females in any particular sample or collection. First, in some species, males emerge from the inactivity period before females and if the population is sampled in this time, males will be more common, e.g., *Ctenophorus fordi* (Cogger 1969, 1978). Second, males may be more active and therefore more likely to be taken in traps, e.g., *Rankinia adelaidensis* (Bamford 1992) and/or they may be more conspicuous and therefore more likely to be taken by hand.

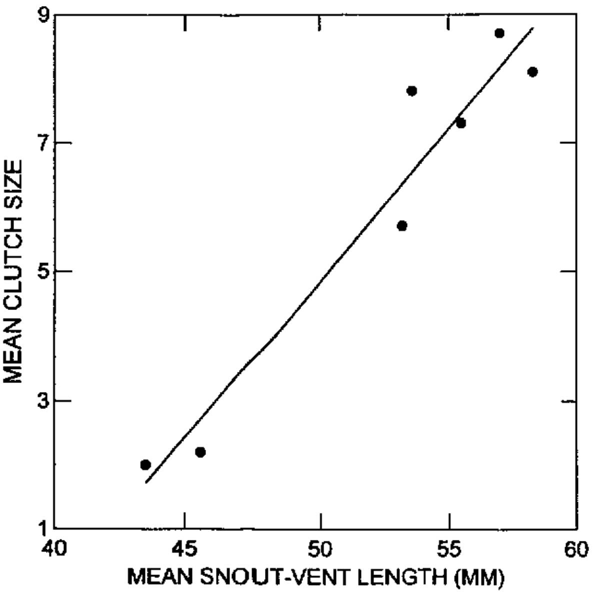

Fig. 10. Mean clutch size versus mean gravid female snout-vent length for six species (one with two subspecies) of *Tympanocryptis*. The equation for the least squares regression line is mean clutch size = –19.04 + 0.48 mean female snout-vent length; ($r^2 = 0.93^{***}$, $n = 7$).

Table 4. Sex ratios in Australian dragons. Sex ratios are calculated as the number of the more common sex/the number of the less common sex, preceded by a "+" sign when males are more common and a "—" sign when females are more common. Sex ratios that are significantly different from parity are in bold. "Sample" refers to the size (age) composition of the sample.

Species	Males/ Females	Ratio	P	Sample	Reference
Amphibolurus					
nobbi	79/40	**+1.95**	<0.001	All	Greer, pers. obs.
Chlamydosaurus					
kingii					
Qld	24/18	+1.33	NS	Adult	Shine and Lambeck 1989
NT	56/16	**+3.50**	<0.001	Adult	Shine and Lambeck 1989; Shine 1990
	96/91	+1.05	NS	≤204 mm SVL	Data in Christian *et al.* 1995
	245/51	**+4.80**	<0.001	>204 mm SVL	Data in Christian *et al.* 1995
Ctenophorus					
caudicinctus					
caudicinctus	29/39	-1.34	NS	Adults	Storr 1967
femoralis	34/23	+1.48	NS	All	Greer, pers. obs.
fordi					
Nymagee					
1961					
Sept.	11/17	-1.55	NS	All	Cogger 1978
Oct.	25/32	-1.28	NS	All	Cogger 1978
1962					
Jan.	13/13	1.00	NS	All	Cogger 1978
Mar.	24/25	-1.04	NS	All	Cogger 1978
May	6/9	-1.50	NS	All	Cogger 1978
Round Hill					
1967					
Mar.	61/51	+1.20	NS	All	Cogger 1978
May	44/48	-1.09	NS	All	Cogger 1978
Aug.	75/10	**+7.50**	<0.001	All	Cogger 1978
Nov.	121/90	**+1.34**	<0.05	All	Cogger 1978
1968					
Feb.	69/73	-1.09	NS	All	Cogger 1978
Mar.	66/95	**-1.44**	<0.05	All	Cogger 1978
Sept.	140/68	**+2.06**	<0.001	All	Cogger 1978
Oct.	109/140	**-1.28**	<0.05	All	Cogger 1978
Dec.	59/55	+1.07	NS	All	Cogger 1978
nuchalis	86/38	**+2.26**	<0.001	Adults	Storr 1966 (as *Amphibolurus inermis*)
	356/280	**+1.27**	<0.01	Adults	Bradshaw and De'ath 1991
reticulatus	32/30	+1.07	NS	Adults	Storr 1966
salinarum	12/11	+1.09	NS	Adults	Storr 1966
Diporiphora					
australis	197/143	**+1.38**	<0.005	All	Greer, pers. obs.
magna	105/64	**+1.64**	<0.001	All	Greer, pers. obs.
Gonocephalus					
boydii	12/13	-1.08	NS	Adults	Torr 1993
spinipes	26/18	+1.44	NS	All	Greer, pers. obs.
Lophognathus					
longirostris	64/37	**+1.73**	<0.01	All	A. Tulloch, pers. comm.
Physignathus					
lesueurii	31/23	+1.35	NS	All	Greer, pers. obs.
Pogona					
barbata	124/59	**+2.10**	<0.001	Adults	Badham 1976
	116/100	+1.16	NS	All	Stauber 1998
minor	10/18	-1.80	NS	Adults	Davidge 1980
vitticeps	151/71	**+2.12**	<0.001	Adults	Badham 1976

Table 4 — *continued.*

Species	Males/ Females	Ratio	P	Sample	Reference
Rankinia					
adelaidensis					
adelaidensis	8/4	+2.00	NS	Adults	Davidge 1980
Nov.	126/40	**+3.15**	<0.001	All	Bamford 1992
Feb.	20/20	1.00	—	All	Bamford 1992
diemensis	38/74	**–1.95**	<0.001	All	Greer, pers. obs.
Tympanocryptis					
tetraporphora	157/133	+1.18	NS	All	This study
	32/37	–1.16	NS	<46.5 mm SVL	This study
	129/95	**+1.37**	<0.05	≥46.5 mm SVL	This study
	37/27	+1.36	NS	Sturt NP	This study

ACKNOWLEDGEMENTS

We thank T. Wickey and J. King for taking the radiographs, and P. Harlow and G. Shea for critically reading versions of the manuscript.

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